

VARIATION IN THE FEMALE FRENULUM IN TORTRICIDAE
(LEPIDOPTERA) PART 1. CHLIDANOTINAE

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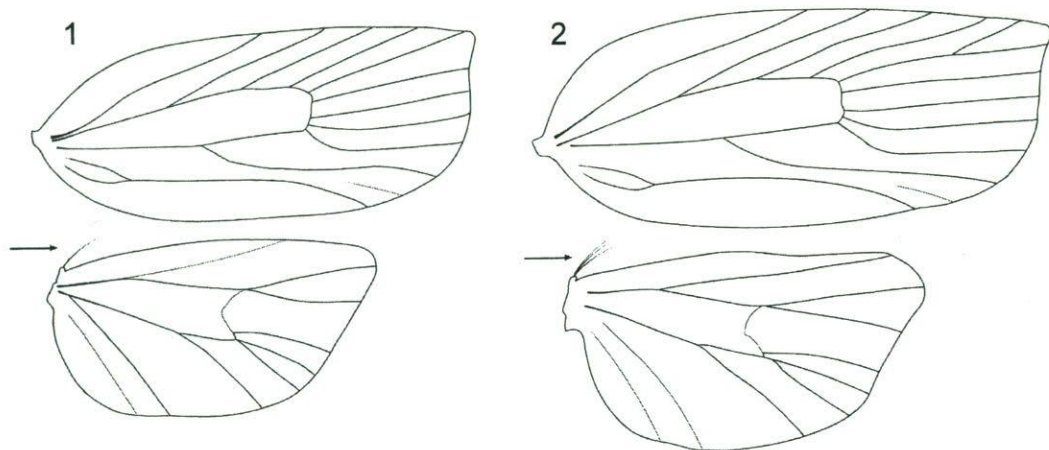
Abstract.—This paper, treating the tortricid subfamily Chlidanotinae (comprised of Chlidanotini, Hilarographini, and Polyorthini), represents the first in a proposed three-part series examining variation in the number of bristles in the frenulum of female tortricid moths. Based on an examination of 86 described species and 11 undescribed species representing 31 genera of Chlidanotinae, the vast majority of females of Chlidanotini and Hilarographini have a two-bristled frenulum, whereas a three-bristled frenulum is the more common state in Polyorthini. When the character states are mapped on a composite, schematic phylogeny of the subfamily, the change from three to two bristles appears to have evolved once at the base of the Chlidanotini + Hilarographini clade and twice within Polyorthini. The consistency of this character within Chlidanotini and Hilarographini provides further evidence for the exclusion of *Mictocommosis* Diakonoff, *Mictopsichia* Hübner, and *Tortrimosaica* Brown and Baixeras from Hilarographini. The distribution of the two-bristled frenulum in Polyorthini appears to support one major clade identified by Razowski (i.e., *Ardeutica* Meyrick, *Polyortha* Dognin, *Pseudatteria* Walsingham, *Polythora* Razowski), plus one outlier, *Cnephasitis* Razowski. In the monotypic *Olindia schumacherana* (Fabricius), five of 18 representatives examined had two bristles, whereas the remainder had three. Minor deviations from this pattern appear to represent intraspecific variation. Preliminary investigations of the character in other tortricid subfamilies suggest a high degree of variation within tribes, genera, and species, with asymmetry common in many individuals. In contrast to the situation in most tortricid taxa, we conclude that variation in the number of bristles in the frenulum is phylogenetically informative in Chlidanotinae.

Key Words: Chlidanotini, Hilarographini, Polyorthini, phylogenetic relationships, character variation

Consistent with the majority of ditrysian Lepidoptera, wing coupling in Tortricidae is accomplished by a spinelike

frenulum arising from the base of the hindwing that extends beneath a complementary structure, the retinaculum, a cuticular flap or group of modified scales in the basal region of the undersurface of

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Figs. 1–2. Wing with frenulum of a male (1) and a female (2) tortricid moth.

the forewing (Scoble 1992). In the tortricid ground plan (Horak 1984), the male frenulum consists of a single bristle and the female frenulum of three bristles (Figs. 1–2).

Reduction in the number of bristles in the female frenulum from three to two was hypothesized to represent a synapomorphy for *Andrioplecta* Obraztsov and *Strophedra* Herrich-Schäffer (Olethreutinae: Graphtolitini) by Komai (1999). However, Brown and Baixeras (2006) suggested that a two-bristled frenulum may be more widespread in Graphtolitini, reporting this character state in the monotypic *Macrocydia* Brown and Baixeras and in one or more species of *Cydia* Hübner, *Pammene* Hübner, and *Grapholita* Treitschke.

Brown (2006) suggested that a two-bristled female frenulum may represent a synapomorphy for Hilarographini + Chlidanotini (Chlidanotinae), but this hypothesis was preliminary, based on a less than comprehensive survey of Chlidanotinae genera. Together these studies (i.e., Komai 1999, Brown and Baixeras 2006, Brown 2006) suggest that variation in the number of bristles in the female frenulum of tortricid moths may be phylogenetically informative at some

levels and within some taxa, but too variable to be useful in others, a common problem diminishing the reliability of characters when inferring phylogenetic relationships.

With the exception of the few studies mentioned above, variation in the female frenulum has been reported rarely in the literature. In order to quantify variation in bristle number and evaluate its phylogenetic distribution, we began a survey of this character over a broad range of tortricid taxa. This paper, treating the smallest of three subfamilies that comprise Tortricidae (i.e., Chlidanotinae), is intended to be the first of a three-part series presenting the findings of this survey. Chlidanotinae are comprised of three tribes (i.e., Chlidanotini, Hilarographini, and Polyorthini) that include about 279 described species and 44 genera. The subfamily is primarily pan-tropical, with its greatest species-richness in the New World tropics.

MATERIALS AND METHODS

Pinned adult moths were examined at 400 \times using a Wild M3Z[®] dissecting microscope under transmitted light from an Intralux 6000[®] illuminator. Although the primary goal was to determine the

number of bristles in the female frenulum, males of each available species were examined as well. Prior to counting the number of bristles in the frenulum, the sex of each specimen was determined by examining the posterior end of the abdomen (i.e., genitalia), which in Tortricidae provides enough morphological features for reliable discrimination of sexes. In a few instances, a number 2 insect pin was used to probe carefully the terminal end of the frenulum to facilitate exposing the bristles. For a variety of reasons (specimens unspread, damaged, etc.), not all specimens could be scored. For each available species, the goal was to examine at least one male and five females; however, many species were represented by far fewer individuals and, in a few cases, only by the holotype. If variation in the number of bristles was observed within a species, additional females were examined. In addition to identified species, we also examined several undetermined species of known genera where males and females were available.

Richard Brown (personal communication) suggested that scanning electron micrographs (SEM) of the base of the frenulum may yield phylogenetically informative characters because of the composite nature of the structure, i.e., both the single bristle of the male and the multiple bristles of the female originate from a base of coalesced bristles. However, capturing SEMs of all species available represents a level of investigation beyond the scope of the present work. Counting the number of bristles present at the distal end of the female frenulum allowed us to complete a much more comprehensive survey, though at a more superficial level. There was little ambiguity regarding the number of free distal bristles.

Components of the frenulum have been referred to as bristles (e.g., Borror et al. 1976), spines (e.g., Zimmerman 1958, Razowski 2008), or acanthae;

however, bristles is the most widely used (e.g., Common 1970, Scoble 1992), so we use this term. Taxonomy follows Brown (2005).

Material used in this study is deposited either in the National Museum of Natural History (USNM), Washington, D.C., or Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica. Marianne Horak provided data on one species from the Australia National Insect Collection (ANIC), Canberra, Australia. All material examined is listed in the appendix except for examples of species represented by males only (i.e., 32 additional species). We relied on the literature for guidance (i.e., to identify taxa that might deviate from the ground plan), but we did not use previously published information if we could not confirm its accuracy.

RESULTS

We examined representatives of 22 species of Hilarographini, 16 of which were represented by females. Sampling included all hilarographine genera except *Idiothauma* Walsingham (i.e., 83% of the described genera). We examined representatives of 37 species of Chlidanotini, 26 of which were represented by females. Sampling included 10 of the 17 described genera (i.e., 59%). We examined representatives of 70 species of Polyorthini, 55 of which were represented by females. Sampling included 15 of the 21 described genera (71%); four of the latter are known only from male holotypes: the monotypic genera *Sociosa* Diakonoff (from Burma), *Lophoprora* Meyrick (from New Guinea), *Scytalognatha* Diakonoff (from New Guinea), and *Pseuduncifera* Razowski (from Mexico).

Males of all specimens examined have a single bristle; the number of bristles in the female frenulum is either two or three. We found intraspecific variation once in Hilarographini (i.e., *Hilarogra-*

pha ribbei (Zeller)) (when the misplaced *Mictocommosis* Diakonoff and *Tortrimosaica* Brown and Baixeras are removed), once in Chlidanotini (i.e., *Archimaga* sp.), and once in Polyorthini (i.e., *Olindia schumacherana* (Fabricius)). Beyond this variation within single species, no genus included species in which females of some had three bristles and others had two.

At the tribal level, virtually all females of Chlidanotini and Hilarographini have a two-bristled frenulum. In Polyorthini, females of *Isotrias* Meyrick, *Histura* Razowski, *Histurodes* Razowski, *Chlorortha* Razowski, *Lypothora* Razowski, *Lopharcha* Diakonoff, *Ebodina* Razowski, *Apura* Turner, *Polylopha* Lower, *Biclonuncaria* Razowski and Becker have three bristles, whereas those of *Ardeutica* Meyrick, *Polyortha* Dognin, *Pseudatteria* Walsingham, *Polythora* Razowski, and *Cnephasitis* Razowski have two bristles (Fig. 3). In *Olindia* Guenée, the number of bristles is variable (two or three).

DISCUSSION

Hilarographini.—Females of Hilarographini have a two-bristled frenulum with the following exceptions: (1) one female of *Hilarographa ribbei* out of the 11 examined; (2) all females of the genus *Mictocommosis* Diakonoff; and (3) all females of the monotypic *Tortrimosaica* Brown and Baixeras. In these exceptions, which are discussed in detail below, the female has three bristles.

In *Hilarographa ribbei*, the three-bristled character state is hypothesized to represent an isolated and apparently rare (for this tribe) example of a reversal to the plesiomorphic condition, reflecting individual variation. The other species of *Hilarographa* examined has two bristles.

A closer examination of *Mictocommosis*, including a review of the genitalia and relevant literature, revealed that the genus does belong in Hilarographini. Male genitalia lack conspicuous hami,

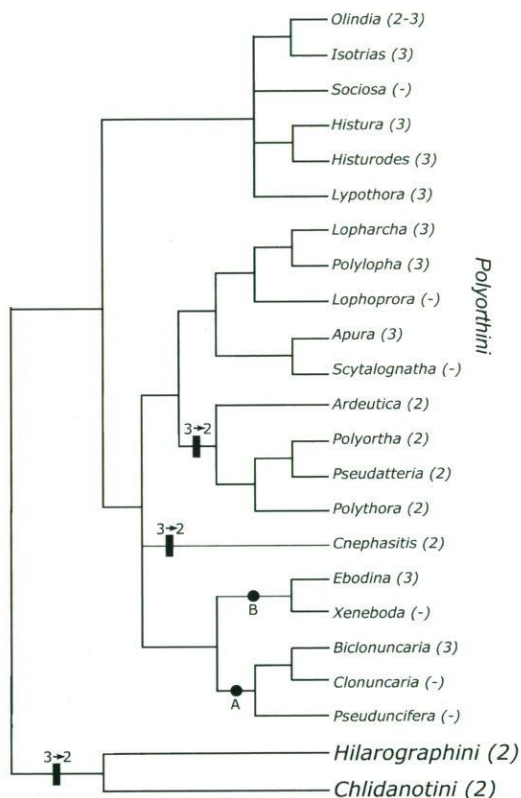


Fig. 3. Composite phylogeny of Chlidanotinae. Relationships among tribes from Tuck (1981), Poinar and Brown (1993), Safonkin (2007), and others; relationships among Polyorthini genera from Razowski (1981); relationships among genera indicated by "A" from Razowski (1999); relationship among genera indicated by "B" from Razowski and Tuck (2000). Number of bristles in parentheses; dash indicates no females examined (*Sociosa*, *Lophoprora*, *Scytalognatha*, and *Pseuduncifera* known from males only).

and female genitalia lack the characteristic "starburst" signum, both of which are considered synapomorphies for Hilarographini + Chlidanotini (Tuck 1981, Razowski 1987, Poinar and Brown 1993). However, this evidence alone is not totally convincing, since these features are lost secondarily in other taxa scattered throughout the tribe. In his description of *Mictocommosis*, Diakonoff (1977) associated the genus with *Mictopsichia* Hübner based on several shared features of the

genitalia, forewing shape, and hind wing pattern. Heppner (1982) suggested that *Mictopsichia* and *Mictocommosis* probably do not belong in Hilarographini, and Horak and Brown (1991) correctly stated that both have typical "tortricine genitalia" rather than chlidanotine genitalia in both sexes, indicating that they do not belong in Chlidanotinae. Heppner (1995) transferred *Mictopsichia* to Euliini, and Brown (2005) treated it as "New Tribe 3" but failed to recognize the association of *Mictopsichia* with *Mictocommosis*. The present data and taxonomic consensus agree that neither of the genera belong in Hilarographini.

Tortrimosaica was assigned provisionally to Hilarographini by Brown et al. (2004) based on larval and pupal characters, which contradict characters of adult morphology. The three-bristled frenulum of *Tortrimosaica* provides additional evidence that the genus likely is placed incorrectly in Hilarographini.

Chlidanotini.—Females of Chlidanotini have a two-bristled frenulum with one exception: one of five females of an undetermined species of *Archimaga* had three bristles. In *Archimaga* sp., the character state of three bristles is hypothesized to represent an isolated reversal to the plesiomorphic condition. Although two other *Archimaga* species were examined, both were represented by males only.

Polyorthini.—Females of nine of the 15 genera of Polyorthini we examined have a three-bristled frenulum. Five genera have a two-bristled frenulum: *Ardeutica* (n = 4), *Polyortha* (n = 13), *Pseudatteria* (n = 13), *Polythora* (n = 1), and *Cnephasitis* (n = 1). In *Olindia schumacherana*, five females examined have a two-bristled frenulum, whereas 13 females have a three-bristled frenulum. Marianne Horak (personal communication) reported that in *Apura xanthosoma* Turner—the only Australian representative examined—five females

had three bristles and one specimen had two bristles on one side and three on the other. She also commented that "at least three of [the] specimens have the third (most distal) bristle somewhat thinner and often also shorter." We noticed some variation in length and thickness of bristles, but did not notice any asymmetry. However, preliminary studies on Olethreutinae and Tortricinae indicate that asymmetry is common in those two subfamilies.

Intraspecific variation in the number of bristles in *Olindia schumacherana* demonstrates that the number of bristles is evolutionary quite labile in some taxa. Given the number of representatives examined (n = 18), it appears that both character states are relatively common within this species.

Phylogenetic implications.—There is no contemporary hypothesis of relationships among the genera of Polyorthini based on cladistic methods. Hence, in order to map the distribution of the two character states, we must rely on a phylogeny that is less than rigorous. If we start with Razowski's (1981) schematic representation of generic relationships within Polyorthini, add his synapomorphy-based phylogenetic hypothesis of the *Biclonuncaria* group of genera (i.e., *Biclonuncaria* Razowski, *Clonuncaria* Razowski, *Pseuduncifera* Razowski, and *Ebodina*) (Razowski 1999), and add the putative sister to *Ebodina* (i.e., *Xeneboda* Razowski and Tuck) (Razowski and Tuck 2000), we have a complete, although tenuous, phylogenetic hypothesis of the genera included in Polyorthini (Fig. 3). If we add this phylogenetic hypothesis among Polyorthini genera to the broadly accepted and synapomorphy-based relationship among the three tribes of Chlidanotinae (Tuck 1981, Horak and Brown 1991, Poinar and Brown 1993, Safonkin 2007), we can map the distribution of two and three bristles on that composite diagram (Fig. 3).

Because the three-bristled condition represents the ground plan for Tortricidae, evolution to a two-bristled state must represent either common ancestry or independent events. If we exclude *Mictocommosis* and *Tortrimosaica* from Hilarographini, as the morphological data strongly suggest (e.g., Heppner 1982, 1995; Horak and Brown 1991), a two-bristled frenulum is remarkably uniform throughout Chlidanotini + Hilarographini and almost certainly represents an additional synapomorphy uniting the two tribes (Brown 2006). With the exclusion of *Mictocommosis* and *Tortrimosaica*, we discovered only two individual character state reversals to the plesiomorphic state: one of 11 females of *Hilarographa ribbei* (Hilarographini) and one of five females of an undetermined species of *Archimaga* (Chlidanotini).

Within Polyorthini, two character state changes are necessary to accommodate the distribution of the character on the tree: the change from three to two bristles at the node supporting the branch that includes *Ardeutica-Polyortha*, and its independent evolution in *Cnephasitis*. Alternatively, it is possible that *Cnephasitis* forms a monophyletic clade with the *Ardeutica-Polyortha* clade, and this hypothesized tree topology would require only a single character state change. The character is polymorphic in *Olindia*.

In conclusion, the number of bristles in the female frenulum is phylogenetically informative in Chlidanotinae. With exceedingly few exceptions, females of Hilarographini + Chlidanotini have two bristles. The three-bristled frenulum of *Mictocommosis* and *Tortrimosaica* provide additional evidence that these two genera should be excluded from Hilarographini. In Polyorthini, the two-bristled condition appears to support a monophyletic clade (i.e., *Ardeutica-Polyortha*), plus *Cnephasitis*.

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Appendix. Numbers represent the number of specimens examined with each character state; sequence of genera alphabetical except for Polyorthini, which follows phylogenetic diagram; "—" indicates no male specimens examined; * taxa misplaced in tribe and subfamily. All specimens deposited in USNM unless indicated otherwise.

Taxon	♂ w/1 bristle	♀ w/2 bristles	♀ w/3 bristles
Hilarographini			
<i>Charitographa mikadonis</i> (Stringer)	1	1	0
<i>Hilarographa ribbei</i> (Zeller)	—	10	1
<i>Hilarographa swederiana</i> (Stoll)	1	4	0
* <i>Mictocommosis argus</i> (Walsingham)	1	0	2
* <i>Mictocommosis nigromaculata</i> (Issiki)	1	0	4
<i>Nexosa picturata</i> Meyrick	—	1	0
<i>Thaumatographa aurosa</i> (Diakonoff and Arita)	1	3	0
<i>Thaumatographa excellens</i> Pagenstecher	—	1	0
<i>Thaumatographa hermatodes</i> (Meyrick)	—	1	0
<i>Thaumatographa jonesi</i> (Brower)	1	5	0
<i>Thaumatographa mesostigmatias</i> Diakonoff	1	1	0
<i>Thaumatographa oenobapta</i> Diakonoff	1	1	0
<i>Thaumatographa opistocapna</i> Diakonoff	1	1	0
<i>Thaumatographa regalis</i> (Walsingham)	1	1	0
<i>Thaumatographa youngiella</i> (Busck)	1	1	0
<i>Thaumatographa zapyra</i> Meyrick	—	1	0
* <i>Tortrimosaica polypodivora</i> Brown and Baixeras	1	0	2
Chlidanotini			
<i>Archimaga</i> sp.	1	4	1
<i>Auratonota aurantica</i> (Busck)	1	7	0
<i>Auratonota dominica</i> Brown	1	4	0
<i>Auratonota hydrogramma</i> (Meyrick)	1	2	0
<i>Auratonota pharata</i> Brown (INBio)	1	2	0
<i>Auratonota magnifica</i> Razowski and Becker	1	1	0
<i>Auratonota petalocrossa</i> (Meyrick) (INBio)	1	2	0
<i>Auratonota</i> sp. 2 (INBio)	1	1	0
<i>Auratonota</i> sp. 3 (INBio)	1	5	0
<i>Caenognosis incisa</i> Walsingham	1	1	0
<i>Heppnerographa arammclaina</i> Razowski	1	2	0
<i>Heppnerographa tricesimana</i> (Zeller)	1	5	0
<i>Meternis ochrolina</i> Meyrick	1	1	0
<i>Monortha corusca</i> (Meyrick)	—	1	0
<i>Monortha pleodontia</i> Razowski	1	1	0
<i>Monortha funestra</i> Razowski and Becker	—	1	0
<i>Monortha</i> sp. 1 (INBio)	1	4	0
<i>Monortha</i> sp. 2 (INBio)	—	1	0
<i>Monortha</i> sp. 3 (INBio)	—	1	0
<i>Pseudocomotis nortena</i> Brown (INBio)	1	1	0
<i>Trymalitis cataracta</i> Meyrick	1	1	0
<i>Trymalitis margarias</i> Meyrick	1	1	0
<i>Trymalitis escharia</i> Clarke	1	5	0
<i>Trymalitis optima</i> Meyrick	1	6	0
<i>Ultrivalva usurpata</i> Razowski	1	1	0
Polyorthini			
<i>Olindia schumacherana</i> (Fabricius)	1	5	13
<i>Isotrias hybridana</i> (Hübner)	1	0	1
<i>Isotrias rectifasciana</i> (Haworth)	1	0	5
<i>Histura cuprata</i> (Meyrick)	1	0	2
<i>Histura limosa</i> (Meyrick)	—	0	1
<i>Histura</i> "obsticata" (ms name)	—	0	1

Appendix. Continued.

Taxon	♂ w/1 bristle	♀ w/2 bristles	♀ w/3 bristles
Polyorthini, Continued			
<i>Histura</i> sp. 1	—	0	1
<i>Histura</i> sp. 2	1	0	5
<i>Histurodes costaricana</i> Razowski	1	0	1
<i>Chlorortha chloromonas</i> Razowski	1	0	3
<i>Lypothora fernaldii</i> (Butler)	1	0	5
<i>Lypothora walsinghami</i> (Butler)	1	0	5
<i>Lopharcha chalcophanes</i> (Meyrick)	1	0	1
<i>Lopharcha curiosa</i> (Meyrick)	—	0	1
<i>Lopharcha psythyra</i> Diakonoff	1	0	5
<i>Lopharcha rapax</i> (Meyrick)	—	0	2
<i>Lopharcha</i> sp. (USNM)	—	0	1
<i>Polylopha epidesma</i> Lower	1	0	1
<i>Polylopha oachranta</i> Diakonoff	—	0	2
<i>Apura xanthosoma</i> Turner (ANIC)	—	0	6
<i>Ardeutica dryocremna</i> (Meyrick)	1	2	0
<i>Ardeutica eupeplana</i> (Walsingham)	1	1	0
<i>Ardeutica spumosa</i> Meyrick	1	5	0
<i>Ardeutica tonsilis</i> Razowski	—	1	0
<i>Polyortha biezankoi</i> Becker	1	6	0
<i>Polyortha bryographa</i> Meyrick	—	2	0
<i>Polyortha chiriquitana</i> (Zeller)	1	5	0
<i>Polyortha chlamydata</i> Dognin	—	1	0
<i>Polyortha clarkeana</i> Razowski	—	1	0
<i>Polyortha evistigana</i> Razowski	—	1	0
<i>Polyortha lyncurion</i> Razowski	1	2	0
<i>Polyortha marodes</i> (Meyrick)	—	1	0
<i>Polyortha myoxa</i> Razowski	1	1	0
<i>Polyortha naevifera</i> Razowski	1	1	0
<i>Polyortha nigriguttata</i> Walsingham	1	5	0
<i>Polyortha symphyla</i> Razowski	—	1	0
<i>Polyortha trochilodes</i> (Meyrick)	—	1	0
<i>Pseudatteria baccheutis</i> (Meyrick)	—	2	0
<i>Pseudatteria canthropa</i> (Meyrick)	—	1	0
<i>Pseudatteria chrysanthema</i> (Meyrick)	1	5	0
<i>Pseudatteria dognini</i> Obraztsov	1	1	0
<i>Pseudatteria heliocausta</i> (Dognin)	1	4	0
<i>Pseudatteria igniflora</i> Meyrick	—	1	0
<i>Pseudatteria leopardina</i> (Butler)	1	5	0
<i>Pseudatteria marmarantha</i> Meyrick	—	6	0
<i>Pseudatteria pantherina</i> (F. and R.)	—	1	0
<i>Pseudatteria splendens</i> (Druce)	1	5	0
<i>Pseudatteria symplacota</i> Meyrick	1	1	0
<i>Pseudatteria tremewani</i> Obraztsov	—	1	0
<i>Pseudatteria volcanica</i> (Butler)	1	5	0
<i>Polythora viridescens</i> (Meyrick)	1	5	0
<i>Cnephasitis dryadarcha</i> (Meyrick)	—	2	0
<i>Ebodina elephantodes</i> (Meyrick)	1	0	5
<i>Biclonuncaria</i> sp. (INBio)	1	0	1